Oceanic islands are not sinks of biodiversity in spore-producing plants

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DOI: https://doi.org/10.1073/pnas.1109119108

Classification: Biological Sciences: Evolution and Population Biology.

Title: Oceanic islands are not sinks of biodiversity in spore-producing plants.

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Author contributions: V.H. and A.V. designed research ; V.H., J.M.G.M. and A.V. contributed to the sampling ; V.H. and J.M. performed research ; V.H., P.S., J.M. and A.V. analyzed data ; and V.H., J.S. and A.V. wrote the paper.

The authors declare no conflict of interest.

Abstract

Islands have traditionally been considered as migratory and evolutionary dead-ends for two main reasons: island colonizers are typically assumed to lose their dispersal power and continental back-colonization has been regarded as unlikely because of niche pre-emption. The hypothesis that islands might actually represent dynamic refugia and migratory stepping stones for species that are effective dispersers, and in particular, for spore-producing plants, is formally tested here for the first time, using the archipelagos of the Azores, Canary Islands, and Madeira, as a model. Population genetic analyses based on nuclear microsatellite variation indicate that dispersal ability of the moss *Platyhypnidium riparioides* does not decrease in the island setting. They further show that, unlike island populations, mainland (Southwestern Europe and North Africa) populations underwent a severe bottleneck during the Last Glacial Maximum. Our results thus refute the traditional view of islands as the end of the colonization road and point to a new perception of North Atlantic archipelagos as major sources of biodiversity for the post-glacial re-colonization of Europe by spore-producing plants.

Keywords: biogeography, dispersal, island syndrome, speciation, refugium

/body

Introduction

Island biogeography has historically been and remains a research area of prime importance for the advance of biology (1). It was in an island setting that Darwin (2) and Wallace (3) presented their theory of evolution by natural selection. It was also in this context that McArthur and Wilson (4) described the 'equilibrium model', according to which biodiversity patterns can be explained by isolation from source populations (immigration) and area size (extinction). Oceanic islands hence appear as natural laboratories of evolutionary and biogeographic processes and Wallace (5) suggested that understanding evolutionary processes within an island context is a key to understanding the same mechanisms in the more complex continental settings.

Theoretical work on population structure has used island models as paradigms for understanding how interactions between gene flow, effective population size and genetic drift influence patterns of genetic variation. Although surprisingly few studies have explicitly tested models of population structure and diversity in island and mainland plant populations (6), theory predicts that island populations should be less variable and more genetically differentiated relative to source populations (7). Differentiation of island populations is further enhanced by one of the most striking syndromes displayed by island taxa, that is, their typical loss of dispersal power as a result of either absence of predation and/or competition in the island setting, or counter-selection against high dispersal ability associated with the risk of massive individual loss to surrounding sea water (8). This process can be fairly rapid. In the annual daisy *Lactuca muralis*, for example, a substantial and significant loss of dispersal power owing to an increase in seed size and decrease in seed volume has been demonstrated over the course of just ten years (9). Continental areas further typically exhibit higher species richness per unit area than islands, leading to the 'niche pre-emption' hypothesis, which proposes that insular colonization is promoted by the available ecological space and continental back-colonization from the islands hampered by inter-specific competition (reviewed in ref. 10).

As a result, islands have traditionally been considered as the 'end of the colonization road'. Wilson (11), in his study of Melanesian islands, for instance stated that a 'taxon can undergo alternate expansion and contraction, with or without speciation, for an indefinite period of time; it can shift its headquarters from a large land mass to a smaller one but not in the opposite direction'. The idea, however, that islands are dead–ends for colonizers, has recently been questioned. Bellemain and Ricklefs (12) emphasized 'the importance of considering reverse colonization for interpreting biogeographic patterns' and highlighted 'the significance that reverse colonization might have for ecological theory in general'. This might be especially true for organisms that are assumed to display a relatively high dispersal power and, in particular, for spore–producing plants.

Bryophytes, which include hornworts, liverworts and mosses, disperse by spores, whole gametophytic fragments, or specialized vegetative propagules, and are precisely the land plants with the widest range of vegetative dispersal devices (13). Phylogenetic and population genetics analyses (see 13 for review), together with correlations between wind and species distribution patterns (14), indicate that bryophytes efficiently take advantage of air currents to achieve long-distance dispersal events. This may account for one of the most striking biogeographic features of the group, that is, its extremely low levels of endemism by comparison with angiosperms (reviewed in ref. 13).

In the present paper, we take advantage of recent developments of coalescent genealogy samplers to bridge the gap between theoretical predictions and actual observations on the genetic consequences of insularity on patterns of diversity and differentiation among island and continental populations. Using as a model the archipelagos of the Canary Islands, Madeira and the Azores, which form a distinct biogeographic unit referred to as Macaronesia (sensu ref. 15), we confront theoretical expectations on patterns of genetic diversity in the moss *Platyhypnidium riparioides*. We aim to determine whether dispersal ability of the latter erode any signature of founding events on extant patterns of genetic variation. We further revisit the idea that island taxa lose their dispersal power by providing the first explicit assessments of the direction and intensity of migration events between islands and continents. Finally, we discuss theoretical and practical consequences of the role of islands as reservoirs or sources of genetic diversity for continents.

Results and discussion

Island populations exhibited significantly lower genetic diversities than continental populations (Table 1), confirming limited available evidence for lower levels of genetic diversity in island than in continental populations (reviewed in ref. 6, but see 16, 17, 18). Population genetic theoretical work indeed predicts that island populations should be less variable relative to source populations because founding populations contains a subset of the genetic variation of the source population (7). This subset is rapidly fixed as a result of the substantial impact of genetic drift and limited gene flow to islands. In contrast to these predictions, however, the coalescence analyses employed here reveal that extant patterns of genetic variation in *P. riparioides* are not consistent with the hypothesis of a bottleneck in the islands (Fig.2c).

Two hypotheses can be formulated to account for the difference in genetic diversity between island and continental settings. First, variation in spatial heterogeneity and habitat diversity of freshwater systems, which was identified as one of the main drivers of genetic diversification in *P. riparioides* (19), is lower in Macaronesian islands than on the continent due to their volcanic origin and the physical properties of watersheds (20).

Second, the low genotypic diversity and evenness values and the significantly higher ($p<0.05$) linkage disequilibrium among loci (0.194) in island vs continental populations (Table 1) point to a shift in mating system towards increased inbreeding and/or clonality on islands. Both ensure rapid population growth following founding events and are fully compatible with several studies that reported similar shifts in mating system from continental dioecious or allogamous ancestors towards insular self-compatible or clonal populations (21, 22). In fact, establishment rates in bryophytes were experimentally shown to be higher from asexual propagules than from spores (23, 24). Asexual propagules allow for early reproduction and, as compared to spores, are less sensitive to habitat quality (23). Asexual reproduction also results in the production of new gametophytes at a faster rate than sexual reproduction (25). These features might be crucial within island settings where the abundance of empty niches might select for fast and efficient dispersal mechanisms at the local scale.

As opposed to other organisms such as diatoms, wherein the absence of any geographic component in genetic variation is suggestive of extremely high dispersal abilities (26), genetic variation in *P. riparioides* is geographically structured [Fst=0.095 between island and mainland

genets, $p<0.001$; Fst=0.177 among regions (Iberian peninsula, Morocco, Canary Islands, Madeira and Azores); $p<0.001$] and exhibits a significant signal of isolation by distance (Table 2). This suggests that, as opposed to previous assumptions (13), the high dispersal ability of spore-producing plants does not necessarily erase any geographical signal in patterns of genetic variation. Two lines of evidence, however, indicate that any signature of bottlenecks in extant patterns of genetic variation in island populations of *P. riparioides* has been eroded by multiple colonization events and/or subsequent gene flow. In fact, although the first two axes of the PCoA of allelic variation are significantly correlated to geographic partitioning of genetic variation ($p<0.001$; Kruskal-Wallis Test, Fig. 3), the mixing of continental and island populations in the ordination diagram and the scattered position of populations from the different archipelagos (Fig. 3) point to recurrent migration events. This might explain why, as opposed to theoretical expectations derived from the island theory, no signal of bottleneck was found in extant patterns of genetic variation in Macaronesian populations of *P. riparioides*.

Most importantly, the present analyses indicate that one of the key island syndromes traditionally found in island colonizers, i.e., the loss of dispersal ability, does not apply in *P. riparioides*. In fact, patterns of isolation by distance are not significantly different among island vs. continental populations, as revealed by the complete overlap in regression slope estimates of Mantel tests (Table 2). These results reinforce the notion that the sea is not a major impediment for migration in mosses (14). The IM analyses further show that the immigration and emigration rates on islands do not significantly differ from each other ($p = 0.7$) (Fig. 4). The results presented here hence suggest that, in contrast to the traditional view of islands as the 'end of the colonization road' (11) and the widely accepted notion that island populations quickly lose their dispersal power (8, and see 10 for review), mosses, and perhaps more generally spore-producing plants, do not lose their dispersal ability in the island setting. Models of wind circulation between the archipelagos, the Iberian Peninsula, and northern Africa indicate that, under the present climate conditions, wind connectivity is comparatively higher from the continents towards the archipelagos than the reverse. In 2001 for example, air currents connecting the Iberian Peninsula to the Canary Islands westwards occurred during 31 days, whereas currents connecting the Canary Islands to the Iberian Peninsula eastwards occurred during 17 days (see Appendix S2). More strikingly, air currents connecting North Africa to the Canary Islands westwards occurred during 251 days, whereas currents connecting the Canary Islands to North Africa eastwards occurred during 15 days. Backward continental colonization might, however, have been facilitated during the arid phases of the last glaciations. Several geomorphological features of Canarian and Maghrebian natural landscapes indeed point towards the dominance of the Westerlies wind regime across the Madeiran-Canarian latitudes (25-30° N) during the glacial periods in the Pleistocene (27). In the meantime, the reiterative emergence of an important array of seamounts (Conception, Seine, Ampere, Coral Patch, Ormonde, etc. (Fig. 1b) potentially served as stepping-stones between the archipelagos and the Iberian and North African mainland (28).

The maintenance of considerable dispersal ability in island bryophytes has important biogeographic and evolutionary implications. First, strong genetic connectivity with the continent hampers genetic isolation. Mallet and Barton (29) demonstrated that even limited gene flow between populations can delay the accumulation of genetic differentiation by drift, and hence, allopatric diversification. This might explain why fewer private alleles were found on islands than

on the continent and, more globally, the low rate of endemism displayed by island bryophytes (see 13 for review).

A second implication of the maintenance of a high dispersal power on islands and, in particular, the high rates of continental back-colonization documented here, is that islands may actually serve as refugia. The present demographic analyses revealed that island population remained constant in size through time. Because of eustatic sea-level transgressions, archipelagos were then almost twice as large as today , thereby increasing the surface available for spore deposition and hosting capacity within a climatically buffered context (Fig. 1). In contrast, a severe bottleneck was detected for continental populations from the western Mediterranean, even in those areas of the Iberian Peninsula that have traditionally been identified as refugia (30). Thus the size of the ancestral population was estimated at log 4.6025 (Fig 2b) as the average medians from the four runs based on ramets and with a generation time of ten years, i.e., approximately 40,000 individuals. The actual population size was estimated at log 3.0975 or approximately 1,250 individuals (Fig. 2a). According to the coalescence inference, and with a generation time of 10 years, the analyses indicate that population size declined at log 4.635, i.e., 43,000 years ago (Fig 2b). A 23,000 year time period was obtained with a generation time of 4 years.

The hypothesis, that continental populations underwent a severe bottleneck during the Last Glacial Maximum (LGM), is further supported by niche modeling analyses. Reconstructions of extant and past (21,000 years BP) potential distribution areas of *P. riparioides* using macroclimate data as predictors (Fig. 1) indeed point to a decrease of suitable areas in the Iberian Peninsula during the LGM. The demise of Iberian populations during the LGM, along with the progressive increase in habitat suitability under present climate conditions, is likely to have increased chances for continental back-colonization by reducing competition for potential colonizers of Macaronesian origin. The historical stability of Macaronesian populations, confirmed by the continuous suitability of habitat conditions since the LGM in the archipelagos (Fig. 1), might have hampered chances for island colonization, potentially accounting for the higher (albeit not significantly) emigration than immigration rates from the islands revealed by the IM analyses. In northern Africa, the extent of habitat suitability rather decreased since the LGM onwards (Fig. 1), rendering the area inhospitable for potential Macaronesian colonizers while making it in the meantime an unlikely source of diaspores. Therefore, despite the geographic proximity and the high wind connectivity between the Canary Islands and northern Africa, Canarian populations exhibit more genetic similarity to Iberian than African ones (Fig. 3). Such genetic connections between Macaronesia and the Iberian Peninsula rather than northern Africa have similarly been interpreted in other land plants as a result of fluctuating habitat suitability in the latter area (31, 32).

The idea that islands are not only sinks of biodiversity, but also sources for continental back-colonization has previously been evoked in a few instances (17, 33). In Macaronesia, back-colonization has been documented in angiosperms. For instance, *Convolvulus fernandesii*, an endemic restricted to Cabo Espichel in Portugal, was resolved as a derived member of a clade of Macaronesian endemic taxa (34). Caujapé-Castells (35) further documented other possible cases of the ‘boomerang’ effect of back-colonization involving Macaronesian angiosperms, although most remain equivocal. In fact, actual evidence for the intensity of island/continent migrations, estimates of population sizes, and the timing of those events are documented here for the first time.

Altogether, our results emphasize a major role for the Atlantic islands as sources of biodiversity for the post-glacial re-colonization of Europe. Many bryophyte species exhibit a striking hyper-Atlantic distribution pattern that is often disjunct between Macaronesia and the western fringe of Europe (15). Such distributions may reflect a similar history with Macaronesia serving as a refugium and a source area for the post-glacial re-colonization of Europe. Furthermore, the striking range disjunctions observed in the Macaronesian bryophyte flora, which include about 8% of the liverworts and 4% of the mosses, indicate that the archipelagos might play a key role as a stepping stone for tropical species in transit towards Europe, eventually resulting in the unique cryptogamic flora of the European Atlantic fringe. While conservation efforts have traditionally focused on the endemic element, the results presented here thus show that the non-endemic element is of prime importance for the evolution of continental biodiversity in the cryptogamic flora, and hence, should be taken into account in conservation planning.

Material and methods

Study area, biological model and sampling design – The Canary Islands, Madeira, and the Azores, offer an ideal setting for investigating questions about the impact of founding and isolation on patterns of genetic structure and diversity because they are all of volcanic origin and exhibit a wide range of distances with the coasts of North Africa and the Iberian Peninsula (Fig. 1).

The moss *Platyhypnidium riparioides* was selected as a model for this study because it has a distribution encompassing the Macaronesian archipelagos, North Africa and Europe. A large aquatic species, *P. riparioides* disperses clonally by whole gametophytic fragments (19) but also by spores, which are produced within an emergent sporophyte that is identical to that of terrestrial species.

In total, 1105 shoots were sampled from 72 localities, including 40 from the southwestern seaboard of Europe and northern Africa and 32 from Macaronesia (Canary Islands : La Palma, Tenerife, La Gomera, Gran Canaria ; Madeira ; and Azores : Sao Miguel, Flores, Faial) (Fig.1, see Appendix S1). For each locality, 1 to 23 patches of 5 individuals separated by > 3 m were collected.

Genotyping – DNA extraction and genotyping followed the protocols described in ref. 36. Each gametophyte was genotyped at 10 microsatellite loci using primers R3, R9, R11, R13, R14, and R17 (36) and four new primer pairs designed from the library of SSR-enriched loci described in ref. 37: R21: F: CCCAAATGCAATCCATGA ; R : GACGAAGCCGAAACTCGT ; R24 : F : TCCTCTTGGTTTGAAAAGG;R: GCAGGTGAAATCGAAAGA; R26: F: CGCACTACCGATCTATGC; R: TTTTGCAGTTTCCTCACC; R35: F: ACTCTCGTCGTTCATTTT; R: AATCAATCGTGAACTTTGCT.

Flow cytometry (Partec PA flow cytometer) revealed the similar genome sizes for specimens from most of the localities sampled in Macaronesia and on the continent. A cytological analysis with Giemsa DNA staining was further performed in order to determine more accurately ploidy levels. Ten to eleven chromosomes, which correspond to the chromosome number most commonly reported for *P. riparioides* and other Brachytheciaceae (37), were counted in several gametophytes from different origins, including populations that exhibited heterozygosity at several microsatellite loci. These results indicate that the rare instances of heterozygosity correspond to duplication events

for individual loci rather than to genome-wide duplication. In line with Stenøien et al. (38), the genotype data were scored as haploid and for the 0.6% of heterozygous genotypes, we took the conservative approach of eliminating the less common allele. Our approach to deleting these alleles may result in a loss of some information but is conservative and would not affect the outcome of analyses.

Data analysis –

Genetic diversity - Preliminary analyses explored genetic variation among the five gametophytes from 120 patches taken at random. The average frequency of the most common genotype in each patch was 93%, suggesting extensive clonality rates within a patch. Therefore, all subsequent analyses were performed using one randomly selected gametophyte per patch, thus resulting in a total of 388 ramets (individual members sharing the same genotype) and 167 genets (all single different genotypes) from 72 localities hereafter referred to as populations.

Genetic diversity per population within each of five areas (Azores, Madeira, Canary Islands, Iberian Peninsula, and Morocco), and for island vs. continental populations, was described by the mean number of alleles, number of private alleles, percentage of polymorphic loci and unbiased expected heterozygosity at the ramet and genet levels using GenAlex 6 (39). Numbers of genotypes, genotypic diversity and their evenness (relative frequency of occurrence of genotypes within a population) were calculated and corrected for sample size with GenoDive (40). Multilocus linkage disequilibrium ("rbard", normalized for sample size) and its deviation from randomly mating reference were calculated using Multilocus 1.3 (41) performing 1000 randomizations.

Allelic richness and private allelic richness corrected for gene sample size were computed with HPRare (42). Significance of differences between insular and continental regions were assessed by performing a Student's *t*-test for the number of private alleles, allelic richness, private allelic richness, percentage of polymorphic loci, gene diversity and multilocus linkage disequilibrium. The other tests (number genotypes, genotypic diversity and evenness) were implemented in the Genodive software through a bootstrap analysis.

Population differentiation and geographical patterns - Global genetic structure was explored by means of a Principal Coordinate Analysis (PCoA) based on a genetic covariance-standardized matrix between each pair of individuals with GenAlex 6. Loci R14 and R35 were discarded due to the presence of missing data. In order to investigate whether geography accounted for the gradients of genetic variation extracted by the PCoA, a Kruskal Wallis test was employed to determine whether specimens from Azores, Canary islands, Morocco and Iberian Peninsula exhibited, on average, significantly different coordinates on the PCoA axes. Genetic partitioning among these regions was further measured by *F*st whose significance was assessed by 999 random permutations of individuals among regions. Spatial autocorrelation analyses were implemented to investigate patterns of genetic variation along gradients of geographic distance. Pairwise kinship coefficients (*F*ij) between individuals, an unbiased estimator with low sampling variance , were computed with Spagedi 1.3 (43) using J. Nason's estimator (44). The significance of the slope of the regression of *F*ij on the logarithm of the spatial distance between individuals was tested by means of 1000 random permutations of population locations (Mantel test). To seek for potential differences in the evolution of kinship coefficients along gradients of geographic distance in island and continental

settings, Mantel tests were also performed among island populations and among continental populations separately.

Migration and demographic history.

The demographic history of *P. riparioides* (current effective population size N_0, past effective population size N_1, and time t since the beginning of the bottleneck) within each of the island and continental settings were explored using a Bayesian method that uses information from the allelic distribution under the stepwise mutation model (SMM) in a coalescent-based framework as implemented by MSVAR 1.3 (45). In these analyses, loci R24 and R35 were discarded because their observed allele size distances were not consistent with the strict SMM model. In the island setting, R26 was also removed because of its monomorphy. The analyses were performed both on the complete dataset (five runs using 152 and 236 ramets for islands and mainland region respectively) and by selecting one individual per population at random (five runs using respectively 32 and 40 individuals for islands and mainland), as advocated by Wakeley (46) and Chikhi et al (47) to reduce potential artifacts associated with local population structure. 1.25 billion steps were performed, with a sampling frequency of 25,000 every 50,000 steps. All runs were performed by using the exponential model of population growth. The first 10% of the saved generations were removed as a burnin (45). Convergence of the runs was checked visually with Tracer 1.5 (48) before combining the results from the different runs. Estimation of the parameter t in those analyses involves the knowledge of the generation time of the species. The model of Wright-Fisher, which is used in the coalescent framework, involves the assumption that successive generations do not overlap. In most organisms, however, this condition is not met, and hence, an average between the age at sexual maturity and life expectancy is used (49). Our observations from experimental cultures suggest that sexual maturity is reached in *P. riparioides* at about 4 years. Regarding the realized life expectancy, Suren et al. (50) showed experimentally that populations of aquatic mosses submitted to a range of streamflow intensity lose 10-12% of biomass after the flood. Since heavy rains occur seasonally every year in the Mediterranean climate region, a colony of *P. riparioides* is completely renewed within a 10-year timeframe. The analyses were hence conducted using a generation length of 4 years for the first ramet run and 10 years for the rest of the analyses

The direction and intensity of migrations between islands and continent were assessed by coalescent simulations using IM (51). IM implements an isolation-by-distance model with two populations and six parameters ($theta_A$, $theta_1$, $theta_2$; t, m_1, m_2).The neutral coalescent model involves random mating, a condition that is unlikely to be met in *P. riparioides* owing to its bisexual gametophytes and putatively high selfing rates (19). We therefore selected one individual from each of 72 localities (40 belonging to the continent and 32 to the island region), as advocated by Lessard and Wakeley (52). Analyses were conducted using 10 Metropolis-coupled Markov chains Monte Carlo with a geometric heating scheme and a burn-in of 150 000 steps. Runs were at least 123 million steps long and the smallest effective sample size (ESS) value reached at least 3000. Convergence of the analyses was monitored by checking the parameter trend lines and repeating each run three times with a different seed value. Analyses were performed using the eight loci that follow the stepwise-mutation model (see above). Over the course of the run, a record was made every 10 steps for parameters estimates such as $m1$ and $m2$, and of the comparison between them. At each recorded step, values of $m1$ and $m2$ are compared and all comparisons provide a

posterior probability estimate that can be used directly as a statistical assessment of comparison between these parameters.

Ecological modeling

To model the current and LGM distribution of *P. riparioides*, we used as presences 269 data points from its entire distribution range collected from herbarium databases at the Real Jardín Botánico de Madrid, the Swedish Museum of Natural History, and the Global Biodiversity Information Facility (53). As background, we randomly selected 10,000 points over the entire distribution area of the species. Data on current and LGM climate were downloaded from the WorldClim website (54), and the layers of current conditions were intersected with the presence and background points to extract the corresponding values of the bioclimatic variables. To avoid multicollinearity, we ran a correlation analysis on the background points and eliminated one of the variables in each pair with a Pearson correlation value >0.8. The final data set included as variables Mean Diurnal Range (BIO2), Isothermality (BIO3), Mean Temperature of Warmest Quarter (BIO10), Mean Temperature of Coldest Quarter (BIO11), Precipitation Seasonality (BIO15), Precipitation of Warmest Quarter (BIO18), and Precipitation of Coldest Quarter (BIO19). Ten cross-validation models for current conditions were generated with Maxent 3.3.3 with the default settings (55), and the resulting average model was projected onto LGM conditions. Validation of models included examination of receiver operating characteristic (ROC) curve and its AUC (area under the curve) parameter.

Wind data from NASA SeaWinds scatterometer were used to perform Anisotropic Cost Analyses, which estimate the minimum accumulative cost of moving from a source cell to every other cell on a raster model considering direction as a parameter (see 14 and 56 for details).

Acknowledgements

Many thanks are due to P. Rasmont, A. Losada Lima, R.M. Ros and C. Vieira for their help in the field. Many thanks also to S. Blake Boles and L. Bukovnik for laboratory assistance and to D. Aigoin and M. Cabria for their help with the analyses. This research was funded by grants 1.5036.11 and 2.4557.11 from the Belgian Funds for Scientific Research (FRS-FNRS), grant C 11/32 from the University of Liège, as well as a fellowship of the Fonds Léopold III. JM is also supported by Ministry of Science and Technology of Spain grant CGL2009-09530-BOS. Support by Duke University (post-doctoral fellowship in evolutionary genomics, Duke University), DAAD, the Humboldt Foundation and the SNSF (Ambizione fellowship) to PS is also greatly acknowledged.

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Figure legends

Fig. 1. Study area and distribution of the sampled populations (stars) of the moss *P. riparioides* in Macaronesia and the neighboring continent, and predicted environmental suitability across time stages, according to the niche model fitted to present locations (dots) and climate. (a) present, (b) 21000 yrs BP. Dots represent specimens used for extrapolating the macroclimatic niche of the species. Colours are representative of the potential suitability with a gradient from white to black, where white is the less suitable and black the most suitable area.

Fig. 2. Posterior probability distribution of demographic parameters of mainland (Iberian peninsula and Morocco) and island (Azores, Canaries and Madeira) populations of the moss *P. riparioides* inferred from the variation of 7 (island setting) and 8 (continental setting) variable nuclear microsatellite loci using the genealogy samplers implemented by MSVAR (61) under the exponential model of population growth. (a) current ($N0$) and ancestral ($N1$) continental population size. (b) time since the decline in population size on the mainland, employing a generation time of ten years. (c) current ($N0$) and ancestral ($N1$) insular population size. Values represent the median (and 95% CI) averaged from 4 independent runs.

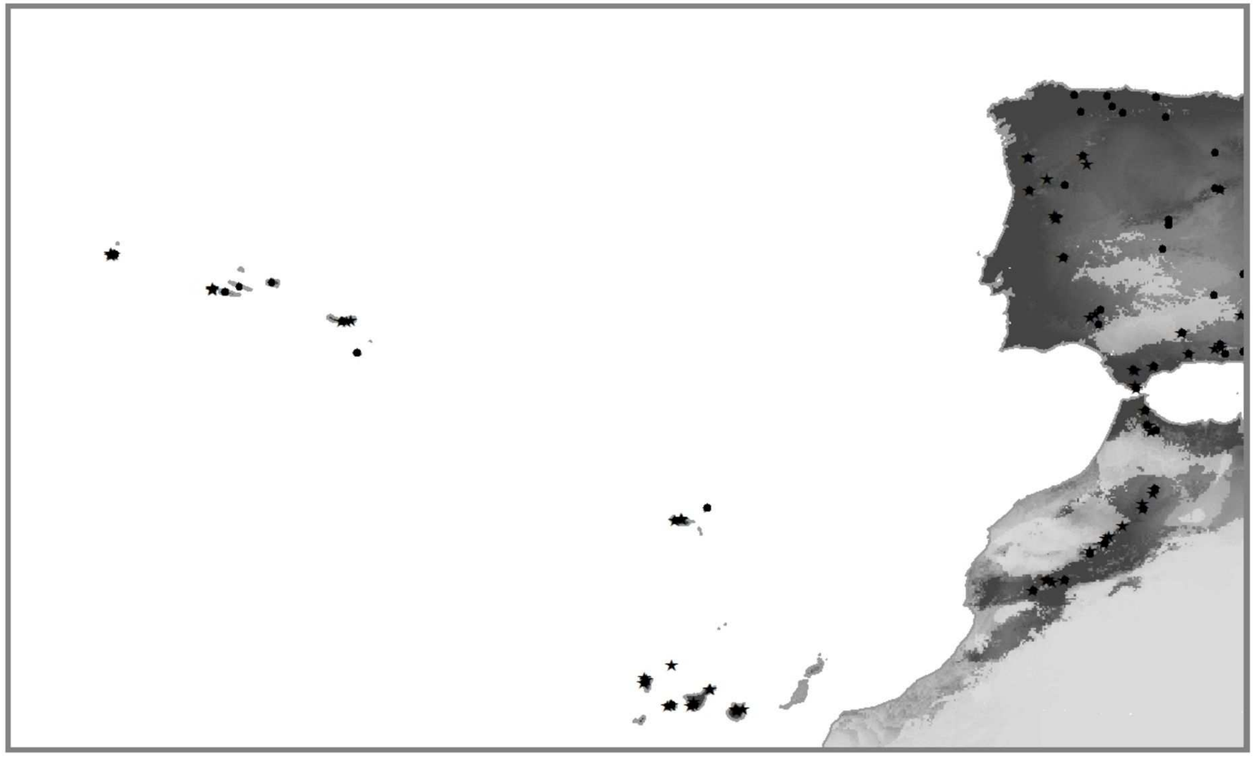
Fig. 3. Principal Coordinate Analysis of allelic variation at 8 microsatellite loci of 388 genets of the moss *Platyhypnidium riparioides* from Macaronesia (Azores, Canaries and Madeira) and the neighboring continent (Iberian peninsula and Morocco).

Fig. 4. Posterior density distribution of the migration rates m between island (32 individuals from Azores, Canaries and Madeira) and continental (40 individuals from Iberian peninsula and Morocco) populations of the moss *Platyhypnidium riparioides* inferred from the variation of 8 nuclear microsatellite loci using the isolation-with-migration model implemented by IM (65). Migration rates are scaled by mutation rate and generation time. Parameter estimates and 90% confidence intervals are averaged over three independent runs.

Table legends

Table 1. Genetic diversity, as measured by the number of private alleles Np, allelic richness Ar, private allelic richness PAr, % polymorphic loci (%P), expected heterozygosity (*H*e) at the genet level, and number of genotypes G, genotypic diversity GD, and evenness E at the ramet level, and multilocus linkage disequilibrium (LD) of 40 mainland (Morocco, Spain and Portugal) and 32 island (Azores, Canaries and Madeira) populations of the moss *Platyhypnidium riparioides* genotyped at 10 microsatellite loci. I≠M test: test of difference between island and mainland values. N: number of analyzed shoots; ^{c}: corrected for sample size ; *, **, *** : significant at p<0.05, 0.01, 0.001 level, respectively.

Table 2. Slope (with 95% confidence intervals in brackets) and significance of the Mantel tests between pairwise kinship coefficients *F*ij calculated from variation at 10 microsatellite loci and pairwise geographic distance among individuals of *Platyhypnidium riparioides* (i) among continental individuals (Iberian Peninsula and Morocco); (ii) among island populations (Azores, Canary Islands, and Madeira); and (iii) for the global dataset.



★ P. riparioides genotyped

● P. riparioides

P. riparioides present suitability

High : 0.961399

Low : 8.99545e-006

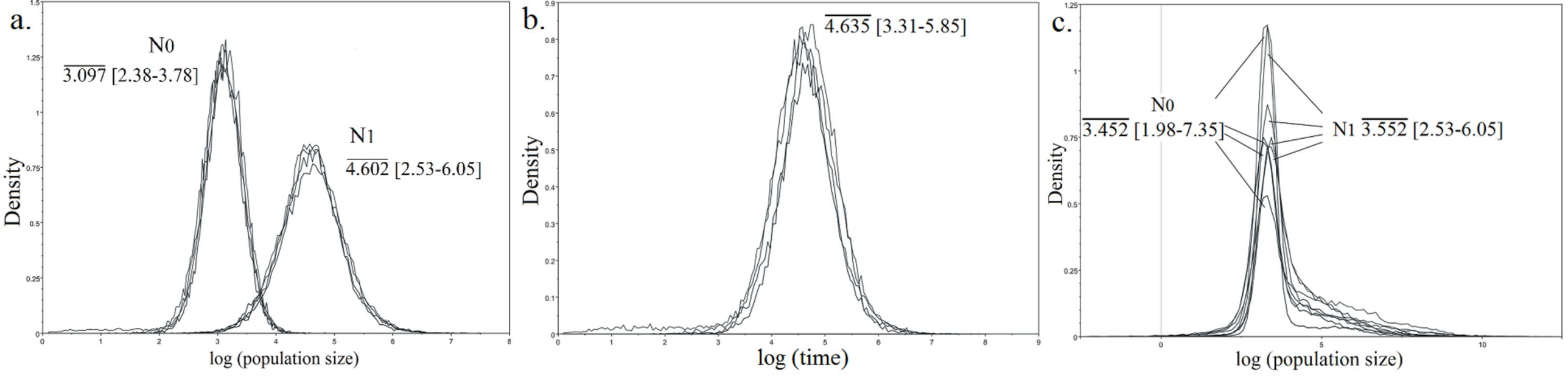
Present time shoreline

LGM shoreline

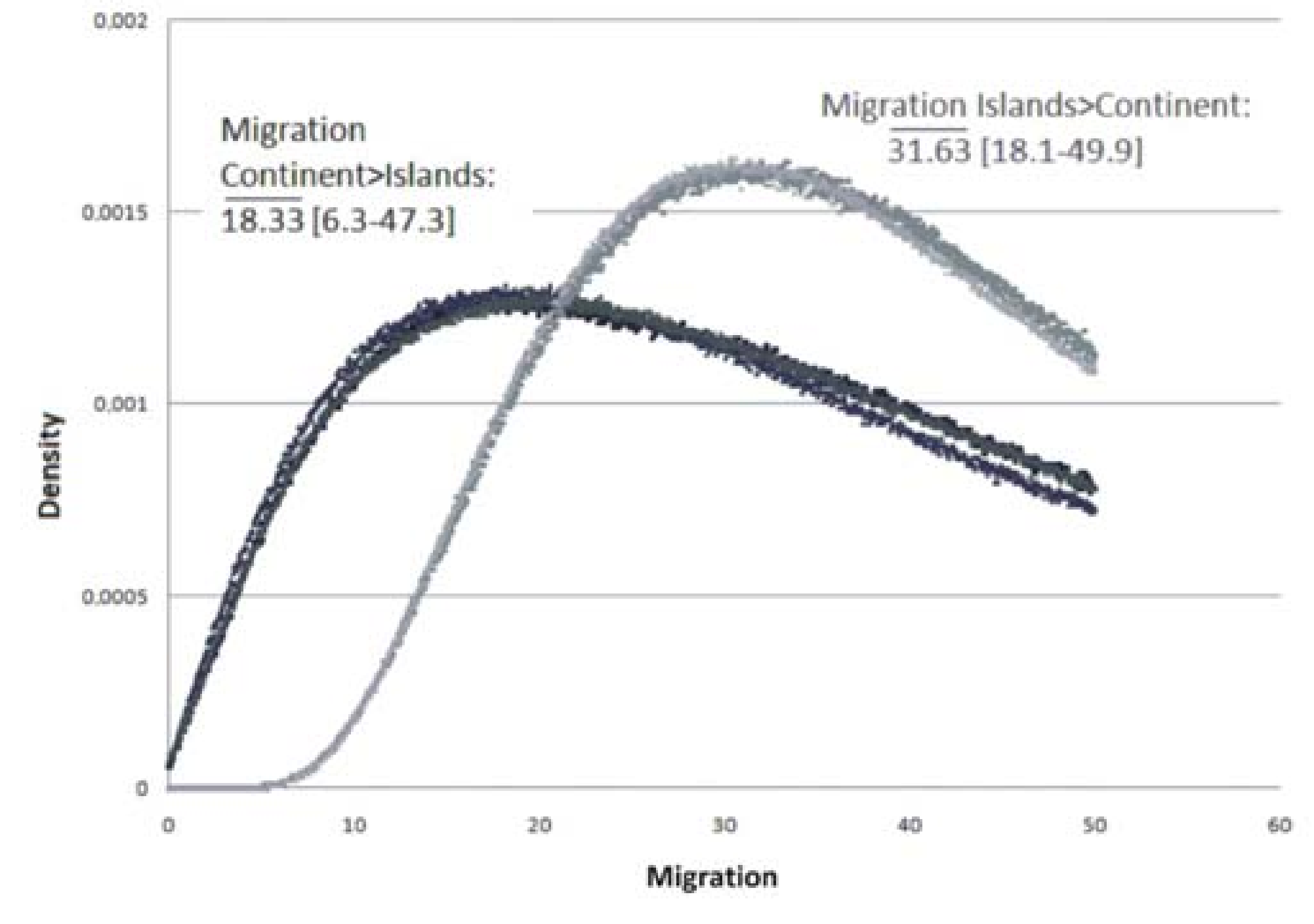
P. riparioides LGM suitability

High : 0.983113

Low : 2.66918e-006


a.
N0
3.097 [2.38-3.78]
N1
4.602 [2.53-6.05]
Density
log (population size)
b.
4.635 [3.31-5.85]
Density
log (time)
c.
N0
3.452 [1.98-7.35]
N1 3.552 [2.53-6.05]
Density
log (population size)

Azores
Canaries
Madeira
Morocco
Spain
Azores
Madeira
Canaries
Morocco
Spain
0.5
0.0
-0.5
-0.5
0.0
0.5
Axis 2 (21.05%)
Axis 1 (27.13%)


Migration
Continent>Islands:
18.33 [6.3-47.3]
Migration Islands>Continent:
31.63 [18.1-49.9]
0.002
0.0015
0.001
0.0005
0
Density
0
10
20
30
40
50
60
Migration

	Island	Mainland	I≠M test
	Genet		
N	50	117	
Np	3	10	*
Ar	2.29	2.61	**
PAr	0.68	1.00	NS
%P	0.425	0.771	***
He	0.199	0.331	*
LD^c	0.194	0.006	*
	Ramet		
N	152 (32)	236(40)	
G	33	116	***
GD	0.93	0.99	***
E	0.38	0.52	*

	Slope log(distance)	Significance
Global	-0.08 [-0.11;-0.05]	P<0.001
Islands	-0.10 [-0.16; -0.04]	P<0.01
Mainland	-0.07 [-0.09; -0.03]	P<0.001